

# THE ROLE OF BIOTA IN THE INITIATION AND GROWTH OF ISLANDS ON THE FLOODPLAIN OF THE OKAVANGO ALLUVIAL FAN, BOTSWANA

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## ABSTRACT

A group of islands of varying size on the floodplain of the Okavango alluvial fan, were studied to establish the processes which lead to the initiation and growth of islands. It was found that islands are initiated by the mound-building activities of the termite *Macrotermes michaelseni*. These termites import fine grained materials to use as a mortar for the construction of epigeal mounds. Their activities create a topographic feature, raised above the level of seasonal flooding, and also change the physical properties and nutrient status of the mound soil. Shrubs and trees are able to colonize these mounds, which results in increased transpiration. As a result, precipitation of calcite and silica from the shallow ground water occurs preferentially beneath the mounds, resulting in vertical and especially lateral growth, causing island expansion. © 1998 John Wiley & Sons, Ltd.

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## INTRODUCTION

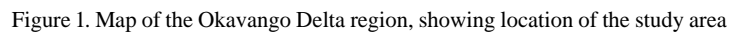
The Okavango alluvial fan of northern Botswana (Figure 1) is situated within grabens related to the East African Rift system (Scholz *et al.*, 1976). The fan has a surface area of approximately 25 000 km<sup>2</sup>, and is the only currently active member of a cluster of fans (Thomas and Shaw, 1991). It has a very low gradient, which averages 1:3000 from apex to toe. Consequently, discharge of the Okavango River onto the fan apex results in the development of extensive permanent swamps in the upper reaches of the fan, and seasonal swamps on the more distal parts. The area of the wetland is in excess of 12 000 km<sup>2</sup>. Water depth in the permanent swamps averages 1.5 m (UNDP, 1977), while in the seasonal swamps it is generally less than 1 m.

The topography of the fan surface is gently undulating, with a local relief of the order of 1.5 to 2 m, creating numerous islands which rise above the water by seldom more than a metre. The size of the islands varies from less than 1 m<sup>2</sup> to many hectares. Islands are relatively few in number in the permanent swamps, but become increasingly abundant down fan, where they eventually merge with seasonal floodplains.

Mound development in seasonally waterlogged soils has been described from many regions of the world, including North America (Dalquest and Scheffer, 1942; Cox, 1984), South America (López-Hernández *et al.*, 1989), central Africa (Gakahu and Cox, 1984) and southern Africa (Lovegrove and Siegfried, 1986), and generally goes under the name Mima mound topography, from the type locality in Mima Prairie, Washington (Cox, 1984). The origin of this type of topography is controversial, and has been attributed to burrowing by rodents (Dalquest and Scheffer, 1942; Gakahu and Cox, 1984), local erosion and entrapment of wind-blown sediment (see Aten and Bollich, 1981), termite activity (Moore and Picker, 1991) and even earthquake effects (Berg, 1990).

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process of precipitation, are confined almost exclusively to islands, due to their sensitivity to flooding and anaerobic soil conditions.

While these processes of island growth in the Okavango are fairly well understood, especially the role played by plants, the processes which initiate island formation are conjectural. Colonization by woody plants requires topographic features above the level of most floods. This study was designed to investigate how such elevated tracts are initiated, and their subsequent growth. It involved an investigation of the physical, chemical and mineralogical properties of soils, and the biological activity, on the floodplain and on several islands of different size.

## METHODS

### *Topographic and vegetation mapping*

The study site (Figure 1) was chosen in an area underlain by homogeneous, sandy soils, and where islands of several sizes are developed in close proximity. A topographic map of an area including four islands of varying size was made using a level and staff (Figure 2a).

Vegetation was sampled at each elevation estimation point, including those localities at which soil was sampled for mineralogical and chemical analysis, using a slight modification of the method described by Meuller-Dombois and Ellenberg (1974). Plant species composition was recorded in circular plots with a radius of 2 m, and abundance was estimated as a percentage of the areal cover on a scale of 1 to 7, representing intervals between 1, 2, 5, 10, 25, 50 and 100 per cent respectively. Groupings in a TWINSPAN cluster analysis (Hill, 1979) provided diagnostic or indicator species which occur in more than 80 per cent of the samples of one group of a division, and fewer than 20 per cent of the samples of the other group. Compilation of the vegetation map was based on this classification of sample plots at known localities and subsequent visual observation.

An estimate of cover for each species was completed on each of the islands in the study area. Size and species composition of several islands in the vicinity of the study site were also measured in order to establish the sequence of island colonization by woody plants.

### *Soil surveys*

Pits and auger holes were put down along transects across four islands of varying size in the study area (Figure 2a), and soils were logged and sampled at at least 20 cm intervals, or smaller intervals where heterogeneity was developed. Auger holes were spaced at approximately 10 m on the islands, because of expected soil variability. Holes were continued in depth until the lack of cohesion of the soil prevented sample retrieval. It was necessary to dig pits on the floodplain because the poor cohesion of the soil made augering impossible. Holes were widely spread on the floodplain as its soils were homogeneous.

### *Soil analysis*

Selected samples were subjected to mineralogical analysis using X-ray diffraction and conventional microscopy, to size analysis by sieving, and to full chemical analysis by X-ray fluorescence spectrometry (XRF). All of the samples were subjected to partial analysis by XRF. The elements Ca, Al, Fe, K and P were determined, and are expressed as oxides, following geochemical convention. Details of these methods have been described elsewhere (McCarthy *et al.*, 1991). The chemical composition was used to calculate a semi-quantitative mineral composition for each sample. Potassium was used to calculate the illite content and excess aluminium was assigned to kaolinite. Iron oxide was assumed to be present only as limonite. Calcite was calculated from the calcium and magnesium contents. A theoretical loss on ignition was then calculated from these mineral proportions and subtracted from the measured loss; the difference was assigned to the organic fraction. The quartz content, which includes amorphous forms of silica, was then calculated by difference from 100. This procedure is semi-quantitative because not all of the potassium is associated with illite, and some iron is included in the clay minerals. Soil pH was measured in mixtures of 10 g of soil and 20 ml of distilled water (Hendershot *et al.*, 1993).

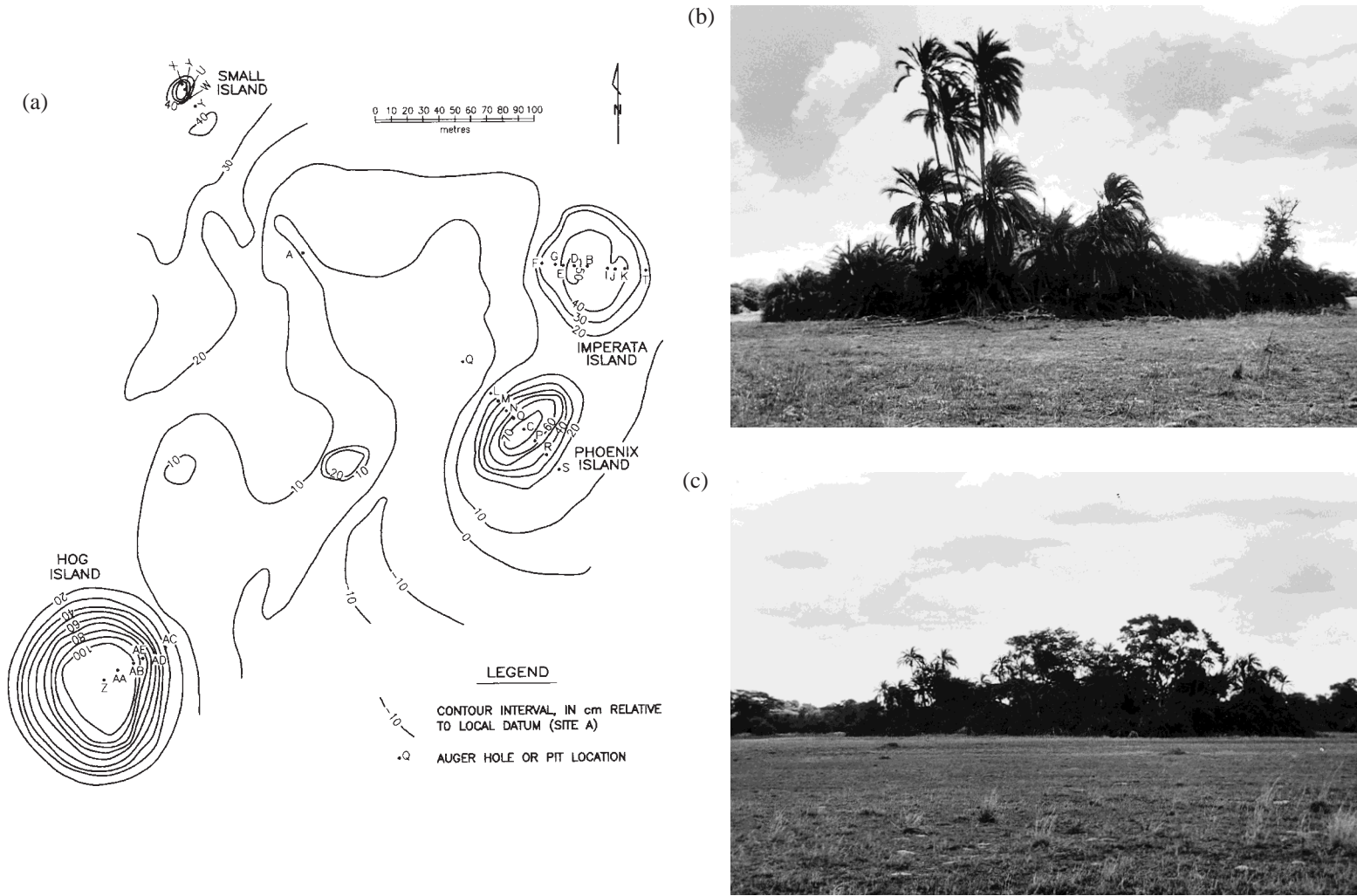


Figure 2. (a) Topographic map of the study area. (b) Phoenix Island. (c) Hog Island

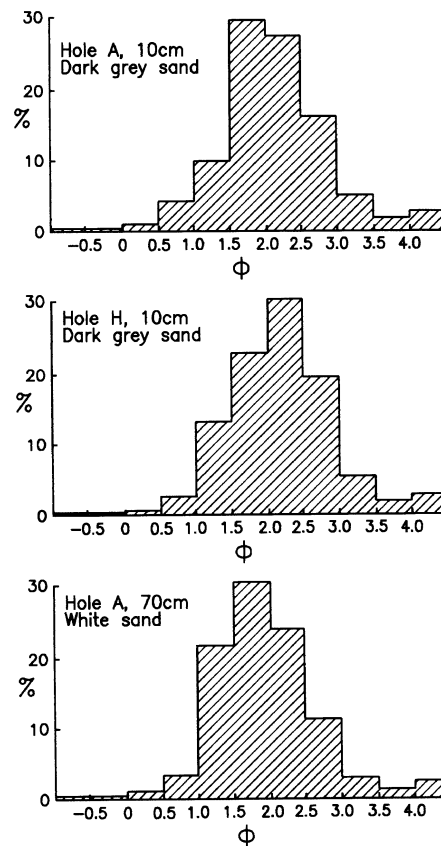


Figure 3. Particle size distribution of floodplain soils

### *Faunal activity*

Presence and activities of a range of soil-dwelling fauna were estimated by visual inspection of the islands and floodplain. Samples of foraging termites were collected from beneath soil-covered runways (carton), and termitaria (epigeal mounds) were opened to determine activity. Evidence of burrowing activity, particularly by mammals, was also noted.

## RESULTS

### *Topography*

The area consists of an extensive, relatively flat alluvial plain with a slight southerly slope of about 1 cm per 10 m, on which numerous mounds occur, which vary in diameter from a few metres to more than 100 m (Figure 2a). The largest mound rises about 2 m above the level of the surrounding plain. Although situated in the seasonal swamps, the study area is slightly elevated as a whole, and would only experience inundation in exceptionally wet years. At these times, the mounds would form islands, and for this reason will be referred to as such here. Four islands were chosen for study, and for convenience were given names, as indicated in Figure 2a. Photographs of Phoenix and Hog Islands are shown in Figures 2b and 2c respectively.

### *Soil profiles*

The floodplain is underlain by clean, well sorted, white sand with an average grain size of 0.2 mm (Figure 3) which extends to a depth of at least 3 m, the deepest excavation made. It is devoid of internal sedimentary structures of any kind and was most probably deposited under aeolian conditions. When dry, the sand lacks

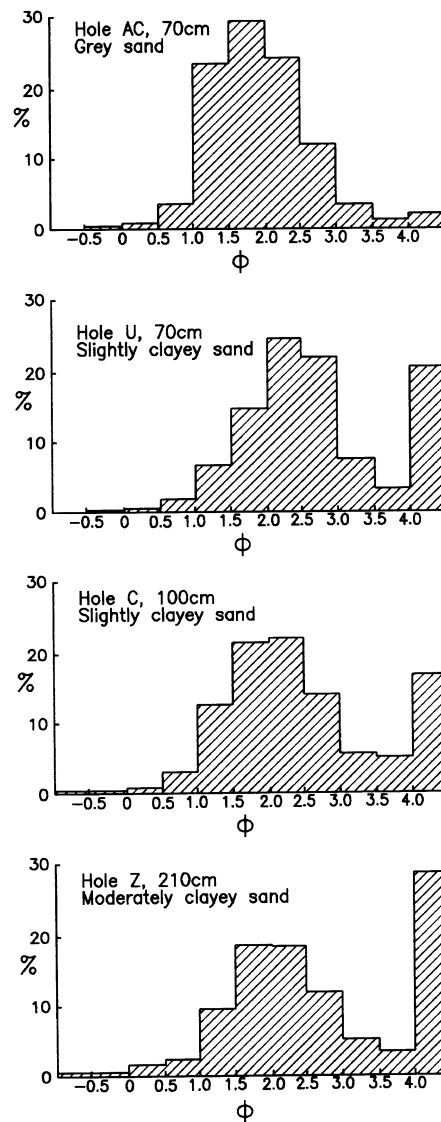


Figure 4. Particle size distribution of island soils

cohesion, although sand in the uppermost metre of the profile is weakly cemented, probably by silica. A dark grey sandy A soil horizon, usually no more than 10 cm thick, is developed at the surface. The presence of abundant roots and a small proportion of fines imparts some cohesive strength to this layer, but organic matter levels are very low. This horizon grades down through a pale grey sand, usually only a few centimetres thick, to the white sand. The size distribution of the surficial sand is the same as the white sand at depth (Figure 3). Locally, especially in the vicinity of the islands, the pale grey layer may thicken to more than a metre. Beneath the islands, a medium to dark grey sand is developed, which has a greater proportion of fines compared to the white sand (Figure 4), and consequently has a slight to moderate clay-like consistency. White streaks and nodules up to 5 mm in diameter are developed in this material, which is confined to the region immediately beneath the islands, and has a lens-like form (Figure 5). The material is underlain by the white sand. In the case of Phoenix island, a root-like extension of the grey material was found to extend downwards below the island. It is possible that similar structures are developed beneath the other islands, but the nature of the sampling was such that these structures could easily have been missed.

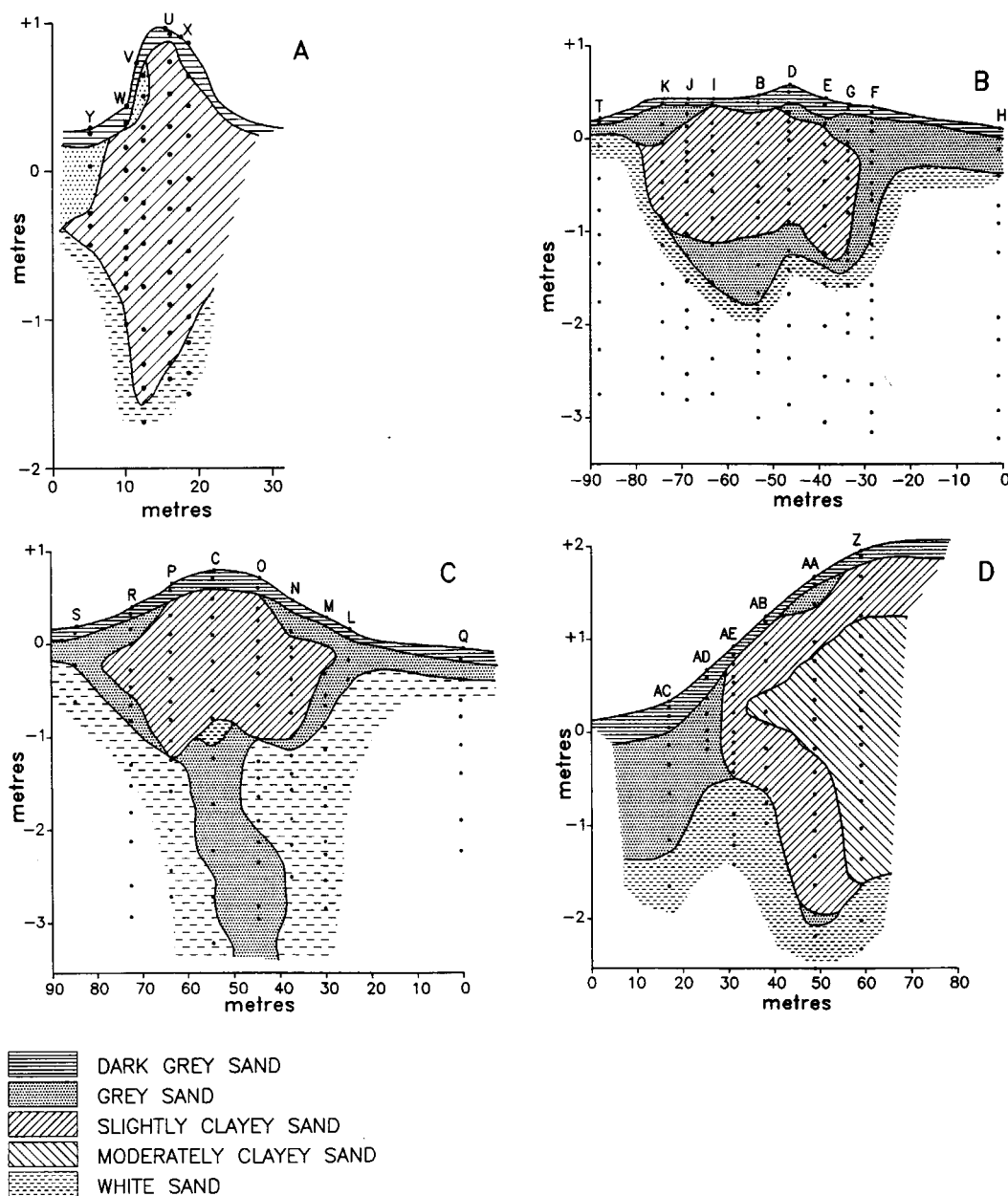


Figure 5. Soil profiles beneath the islands. (A) Small island; (B) Imperata island; (C) Phoenix island; (D) Hog island. Dots show sampling points in each of the auger holes or pits. Vertical axis is sample elevation relative to local datum (Figure 2a), and horizontal axis shows horizontal distance between holes. See Figure 2a for location of profiles

### *Mineralogy and chemistry of soils*

Complete analyses of representative samples of the soil types encountered are listed in Table I. The mineralogy of the soil is very simple, being dominated by quartz, with minor calcite, clays (kaolinite and illite) and limonite (Table I).

The white and grey sands (Table I, columns 4 and 5) contain in excess of 97 per cent silica, reflecting the dominance of quartz. The dark grey sand (Table I, columns 1 to 3), which forms the A soil horizon, has a slightly lower silica content and higher aluminium content than the white sand, with slightly more clay and less quartz.

Table I. Chemical analyses of representative soil samples (data expressed in weight percentage). 'Hole' refers to the location of the sample (Figure 2a) and 'Depth' is depth below surface

Material	A soil horizon			White sand	Grey sand	Slightly clayey sand			Med. clayey sand
Location:	Floodplain			Floodplain		Small island	Phoenix island	Imperata island	Hog island
Hole:	A	H	Q	A	AC	U	C	I	Z
Depth (cm):	10	10	10	50	70	70	100	130	210
SiO <sub>2</sub>	95.13	93.98	95.21	97.21	98.20	88.34	87.38	79.29	76.07
TiO <sub>2</sub>	0.19	0.18	0.19	0.18	0.19	0.24	0.22	0.21	0.20
Al <sub>2</sub> O <sub>3</sub>	1.78	1.63	1.74	1.40	1.34	3.92	33.46	4.07	3.17
F <sub>2</sub> O <sub>3</sub>	0.57	0.52	0.61	0.54	0.48	1.13	1.87	2.29	2.02
MnO	0.06	0.07	0.06	0.06	0.06	0.06	0.07	0.09	0.10
MgO	0.32	0.28	0.27	0.24	0.23	0.37	0.59	0.60	0.93
CaO	0.00	0.02	0.02	0.00	0.00	1.68	1.74	4.29	7.19
Na <sub>2</sub> O	0.04	0.02	0.03	0.03	0.03	0.32	0.11	0.05	0.38
K <sub>2</sub> O	0.14	0.11	0.12	0.11	0.08	0.23	0.28	0.27	0.47
P <sub>2</sub> O <sub>5</sub>	0.09	0.08	0.08	0.09	0.08	0.07	0.08	0.09	0.13
LOI	1.27	3.00	2.04	0.39	0.24	3.93	4.38	7.61	9.47
TOTAL	99.59	99.89	100.36	100.23	100.14	100.29	100.18	98.85	100.30
Illite	1.2	0.9	1.0	0.9	0.7	2.0	2.4	2.3	4.0
Kaolinite	3.4	3.2	3.4	2.6	2.7	8.0	6.5	8.1	4.1
Limonite	0.6	0.5	0.6	0.5	0.5	1.1	1.9	2.3	2.0
Calcite	0.6	0.6	0.6	0.5	0.5	3.8	4.3	8.9	14.8
Quartz	93.8	92.6	93.2	95.4	95.6	84.1	83.6	76.1	73.0
Organic material	0.5	2.2	1.2	0	0	1.0	1.4	2.4	2.1

The grey colour is due to a concentration of organic material. Slightly clayey sand (columns 6 to 8) is enriched in both aluminium and calcium, due to increased clay and calcite contents, and also in limonite. The moderately clayey sand (column 9) has a similar aluminium content to the previous samples, but is considerably enriched in calcium due to a higher calcite content and also has a slightly higher limonite content. The increase in clay and calcite is associated with a marked increase in the  $-4\phi$  size fraction (Figure 4), indicating that these materials are very fine grained.

An indication of the spatial distribution of clay beneath the islands can be obtained from the distributions of aluminium (Figure 6). The white sand which envelops the islands is very low in Al, reflecting negligible clay content, but in all cases there is a concentration of Al beneath the islands. The smallest island has the highest Al contents, while the largest island has the lowest.

The spatial distribution of calcium beneath the islands, which reflects the distribution of calcite, shows that the enveloping white sand contains negligible calcite and, like clay, calcite is also concentrated beneath the islands (Figure 7). However, unlike Al, the smallest island has significantly lower Ca contents than the largest island. The zones of elevated Ca and Al levels correspond to the distribution of clayey sand (Figures 5, 6 and 7). Clay and calcite are both very fine grained, and their presence in the sandy soil imparts a clayey texture to the sand.

There is no apparent correlation between the Ca and Al contents beneath the islands (Figure 8). However, on closer inspection it can be seen that a correlation does exist for samples with very low Ca contents. The implication is that there is an underlying correlation between clay content and calcite content, but some samples have had additional calcite added.

The distribution of limonite can also be examined in plots of Al against total iron (Figure 9). Good correlations are evident for each of the islands, but the plots show a range of gradients which tend to steepen with island size. There is a close correspondence between clay content and limonite content, but each of the islands has a different ratio of clay to limonite, with Imperata and Phoenix islands having a very similar ratio. These plots do not trend towards the origin, which is simply a reflection of a small amount of iron oxide associated with the dominant quartz component.



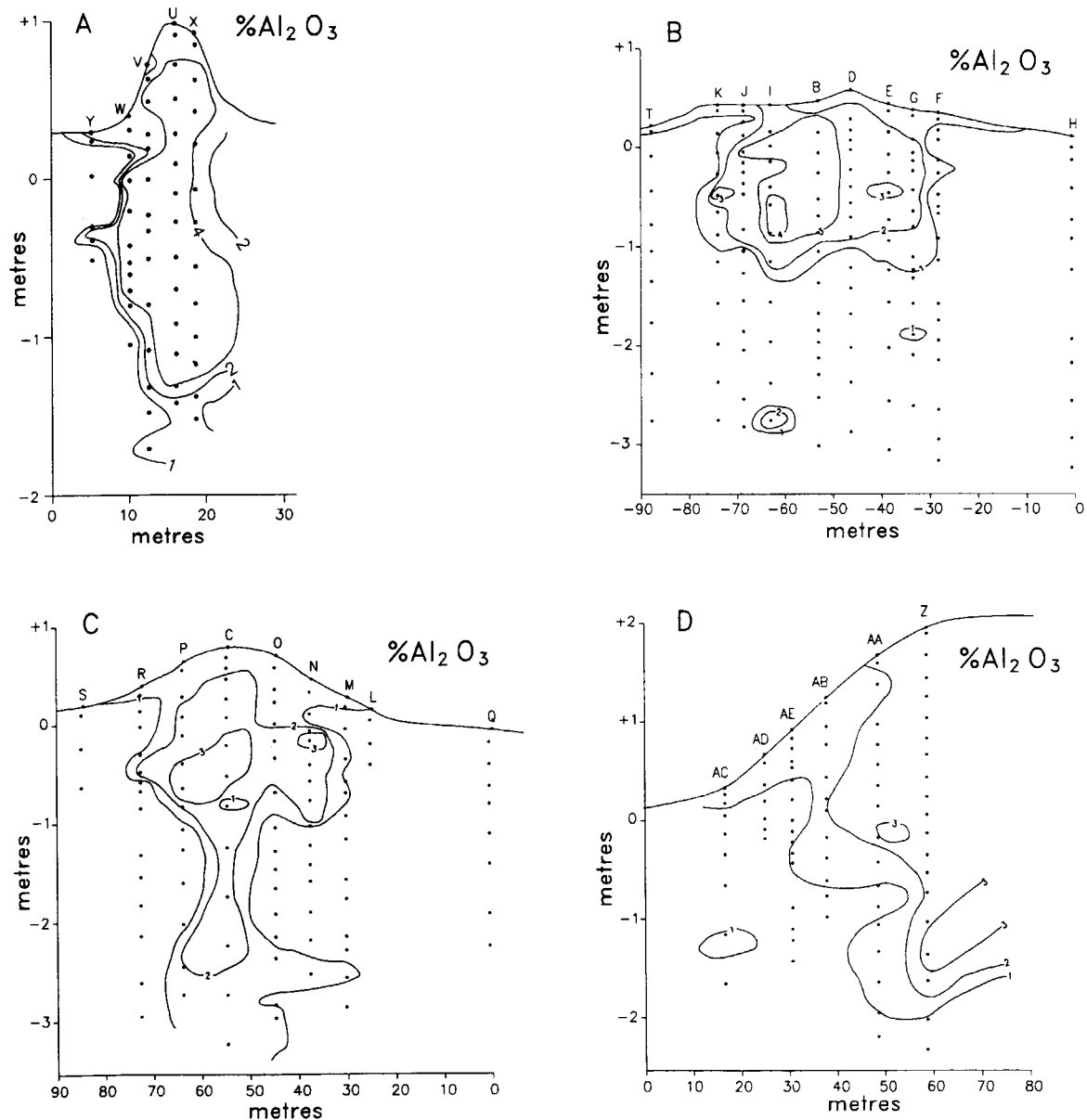


Figure 6. Distribution of aluminium beneath islands; concentration contours in wt per cent  $\text{Al}_2\text{O}_3$ . (A) Small island; (B) Imperata island; (C) Phoenix island; (D) Hog island. Dots show sampling points in each of the auger holes or pits. Vertical axis is sample elevation relative to local datum (Figure 2a), and horizontal axis shows horizontal distance between holes. See Figure 2a for location of profiles

The origin of correlation between limonite and clay, in the absence of a similar correlation between clay and calcite, is enigmatic. Previous studies (e.g. McCarthy *et al.*, 1991) indicate that the Fe/Al ratio in Small island is typical of other areas in the Okavango region. Fe appears to have been added to island soils in the study area, but this iron must be closely associated with the clays, perhaps as a limonite coating. Limonite shows no such association with calcite, however. The Fe/Al ratio appears to reflect the size and hence age of the island, suggesting that biological activity is responsible for iron accumulation, although clay may act as a nucleus for iron precipitation. Iron staining was frequently observed in the soil surrounding roots, supporting biological accumulation.

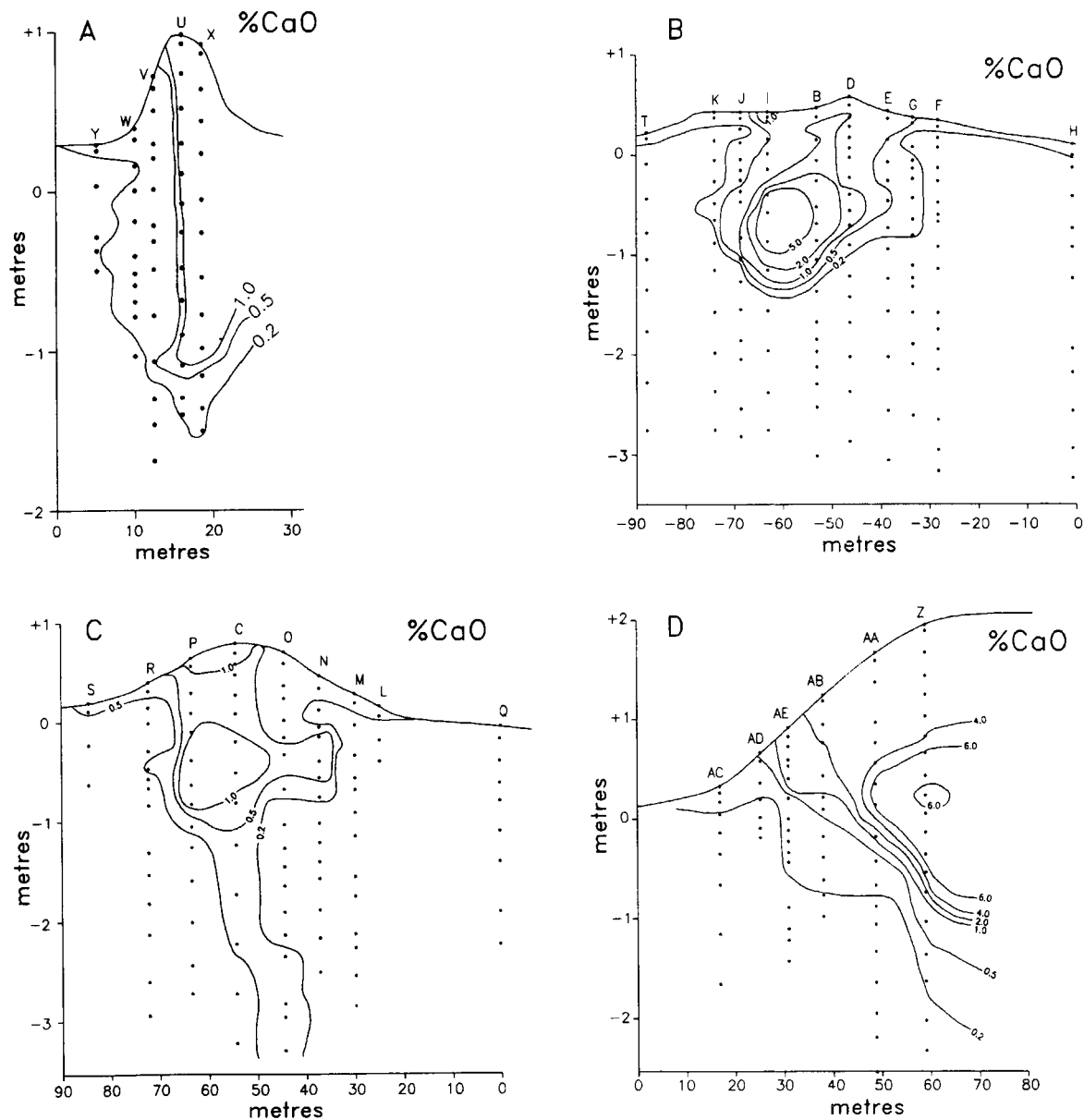


Figure 7. Distribution of calcium beneath islands; concentration contours in wt per cent CaO. (A) Small island; (B) Imperata island; (C) Phoenix island; (D) Hog island. Dots show sampling points in each of the auger holes or pits. Vertical axis is sample elevation relative to local datum (Figure 2a), and horizontal axis shows horizontal distance between holes. See Figure 2a for location of profiles

The total potassium concentration of floodplain soils is very low, rarely exceeding 200ppm. Potassium is a constituent of illite and would therefore be expected to be enriched in island soils, and moreover to correlate with the Al content of the soils. Such a correlation is evident in the case of Small island (Figure 10), and the slope corresponds to a ratio of kaolinite to illite of about 5. Imperata and Phoenix islands show a slight enrichment in potassium relative to Small island, while the soils of Hog island show pronounced enrichment in potassium. The spatial distribution of potassium (Figure 11) closely follows that of aluminium in the case of Small, Imperata and Phoenix islands. However, on Hog island, potassium is concentrated in the upper part of the soil profile and towards the island centre.

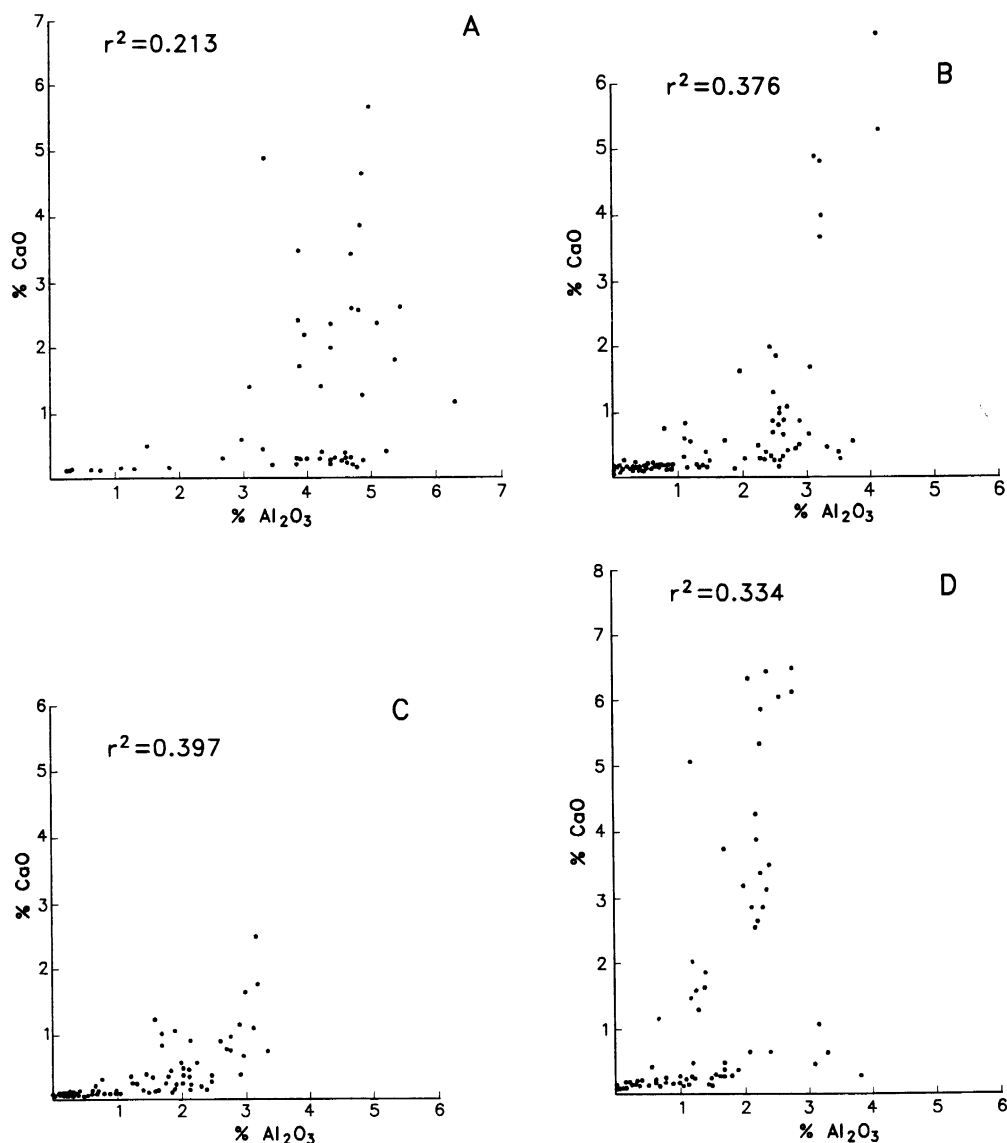


Figure 8. Scatter diagram of Al against Ca in island soils. (A) Small island; (B) Imperata island; (C) Phoenix island; (D) Hog island

The total phosphorus content of floodplain soils is also very low, with  $\text{P}_2\text{O}_5$  content rarely exceeding 200 ppm, except in the A horizon, where concentrations are generally between 200 and 300 ppm. In contrast, island soils show a pronounced enrichment in phosphorus (Figure 12), particularly in the uppermost parts of the soil profile. Hog island shows the greatest enrichment in phosphorus, and  $\text{P}_2\text{O}_5$  concentration attains 7000 ppm in the upper parts of the soil profile on the island fringe.

In view of the very large geochemical database and its complex variability, an  $R$  mode factor analysis (Jöreskog *et al.*, 1976) was carried out on the combined data from all islands. The varimax rotated factor matrix is shown in Table II, together with eigenvalues and cumulative variance. Four factors account for 96.9 per cent of the variation in the data. Factor 1, which accounts for 63.8 per cent of the variance, is associated mainly with Ca, while Factor 2, responsible for 18.4 per cent of the variance, is associated principally with Fe. Factor 3 is principally associated with P and Factor 4 with Al. K is not associated with any particular Factor, but has moderate loadings in all Factors.

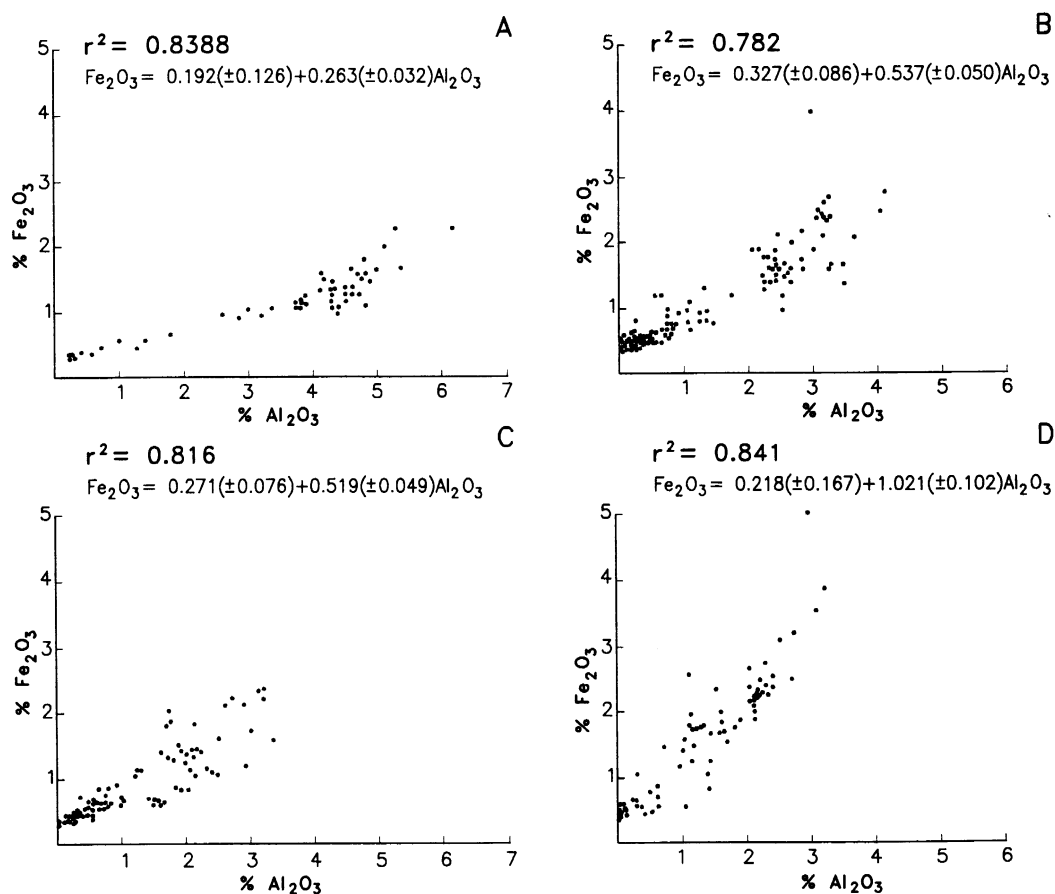


Figure 9. Scatter diagram of Fe against Al in island soils. (A) Small island; (B) Imperata island; (C) Phoenix island; (D) Hog island. Equations fitted using least squares techniques are shown, together with 95 per cent confidence limits on the coefficients

Floodplain soils are generally acidic, while island soils are alkaline. The pH of surface soils on islands is around 7 but pH rises rapidly with depth to above 9 on all islands, thereafter decreasing slowly (Figure 13). A comparison of Figures 6, 7 and 13 suggests that pH is spatially unrelated to calcite or clay content.

#### Classification of vegetation

Cluster analysis grouped the vegetation samples ( $n=76$ ) into four communities (Figure 14). The first division (eigenvalue=0.728) was based on the presence of several terrestrial species in the positive group ( $n=2$ ), including the woody plants *Capparis tomentosa* and *Lonchocarpus capassa*. The grass *Setaria verticillata*, found only in truly terrestrial situations, was also an indicator of this group. Several other terrestrial species were found only in samples in this group, which are typical of the interior regions of large islands on the floodplains of the Okavango Delta. These samples constitute what is referred to as the 'island interior community'.

There were no indicator species associated with the samples in the negative group, but these samples were divided into two groups on the second level of division (eigenvalue=0.513). The indicator species *Eragrostis inamoena*, typical of seasonally flooded habitats, was associated with the samples in the negative group ( $n=61$ ), while the grass *Cynodon dactylon*, with a cover of greater than 5 per cent was an indicator species in samples in the positive group ( $n=13$ ). The grass *Imperata cylindrica*, typical of intermittently flooded habitats, was a preferential species of samples in the positive group. *Cynodon dactylon* typically occurs in slightly drier situations than *I. cylindrica*. Species associated with the samples in the negative group are typical of floodplain habitats, where inundation is frequent (annually), and lasts for several months during the flood season. In

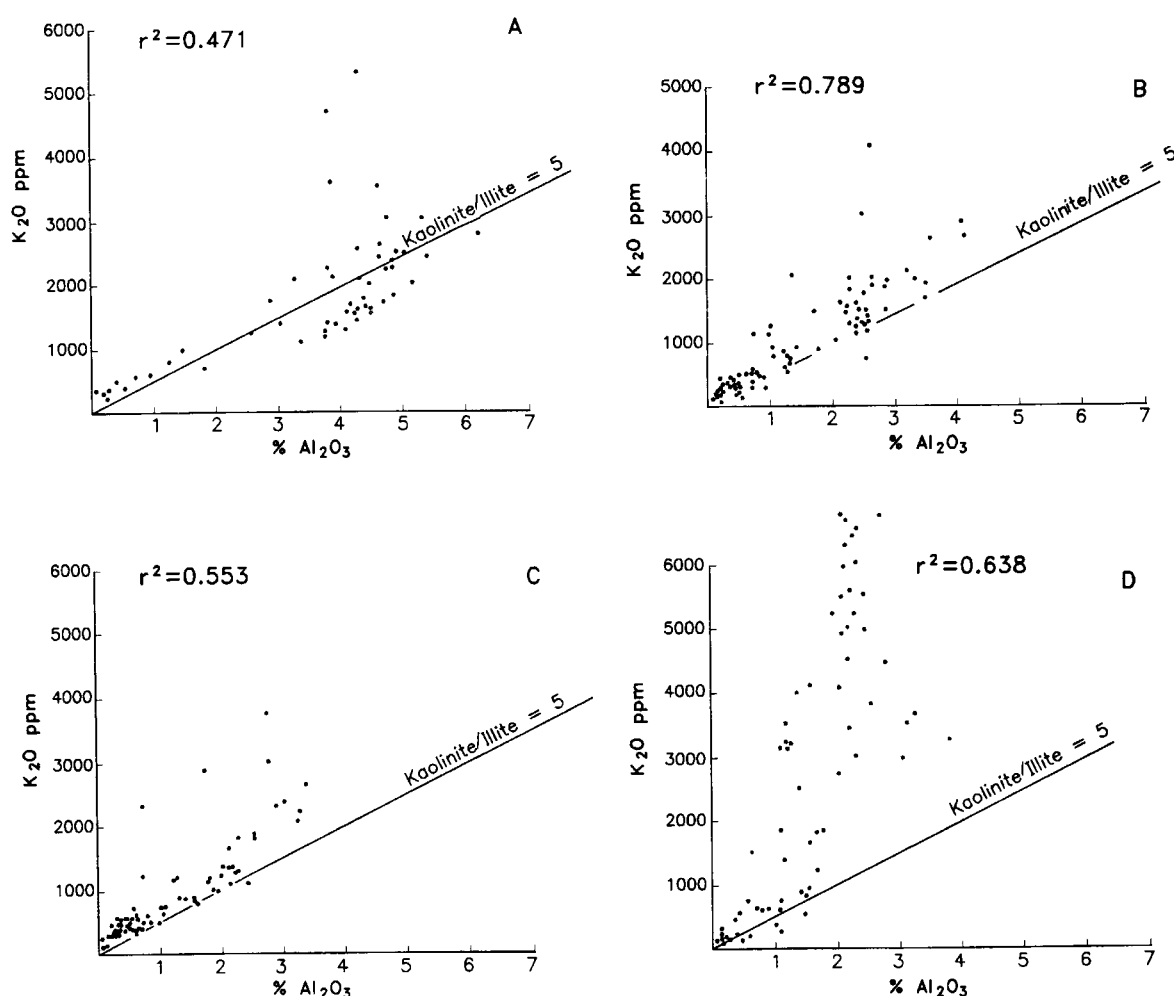


Figure 10. Scatter diagram of Al against K in island soils. (A) Small island; (B) Imperata island; (C) Phoenix island; (D) Hog island

particular, the sedge *Scirpus corymbosus*, which is typical of seasonal as well as permanent swamp habitats, indicates that flooding is prolonged. The grasses *Panicum repens* and *Eragrostis inamoena* are also typical habitats which are flooded for several months of the year. However, the occurrence in the community of the daisy *Ethulia conyzoides*, which is more typical of dryland situations and which tends to colonize disturbed areas rapidly, suggests that flooding has not taken place in the study area for several years prior to the study.

Samples in the negative group at the second level of division were divided into two groups at the third level of division (eigenvalue=0.260). This low eigenvalue, the lack of indicator species, and no distinct differences between samples in these two groups, suggests that this division does not distinguish the two communities. This community is referred to as the 'lower floodplain community'.

Samples in the positive group at the second level of division were divided into two groups at the third level of division (eigenvalue=0.486). Samples in the positive group ( $n=2$ ) were indicated by the presence of *Phoenix reclinata* with a high cover (greater than 10 per cent), while those in the negative group were indicated by the presence of *Cynodon dactylon* with a high cover (greater than 5 per cent). This division distinguishes well established island fringes with a high cover of *P. reclinata* from those which are transitional between island and floodplain, and these communities are referred to as the 'island fringe community' and 'upper floodplain community' respectively.

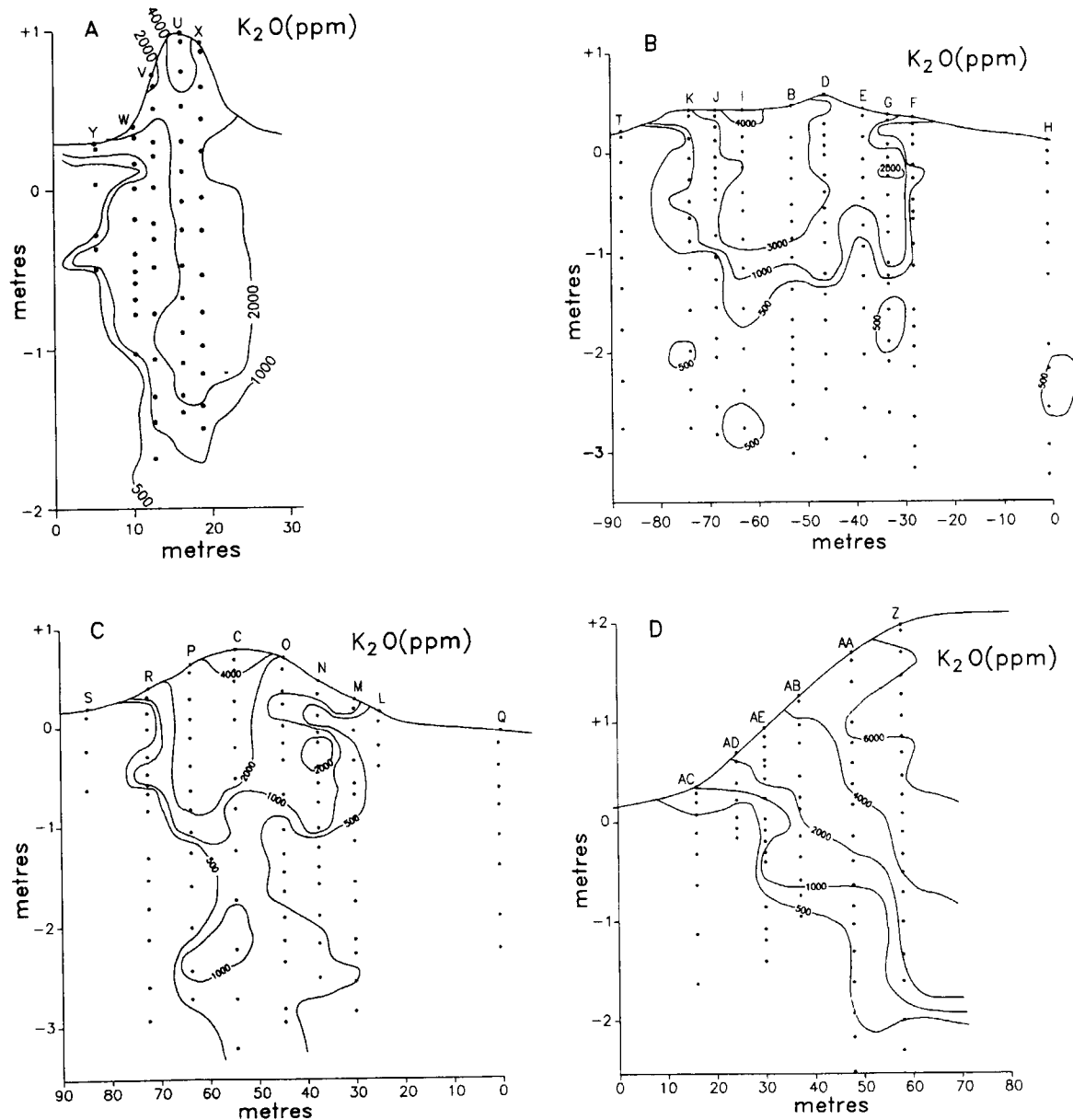


Figure 11. Distribution of potassium in island soils; concentration contours in ppm  $K_2O$ . (A) Small island; (B) Imperata island; (C) Phoenix island; (D) Hog island. Dots show sampling points in each of the auger holes or pits. Vertical axis is sample elevation relative to local datum (Figure 2a), and horizontal axis shows horizontal distance between holes. See Figure 2a for location of profiles

### Vegetation distribution

The approximate cover of individual species in samples taken at intervals across each of the islands indicates a zonation across islands (Figure 15). *Eragrostis inamoena*, *Panicum repens* and *Scirpus corymbosus* occur at lower elevations in areas which are flooded for the most prolonged periods, whereas *Cynodon dactylon*, *Imperata cylindrica* and *Setaria sphacelata* occur at higher elevations in areas not flooded for long periods. Woody plants, including the palm *P. reclinata*, species of the genus *Acacia* (*A. sieberana* and *A. tortillis*), *Maytenus senegalensis* as well as numerous other species, occur at elevations which are never flooded.

Across the study area, the lower floodplain community occurs on low-lying ground flooded for prolonged periods, the upper floodplain community on higher ground flooded intermittently, and the island interior

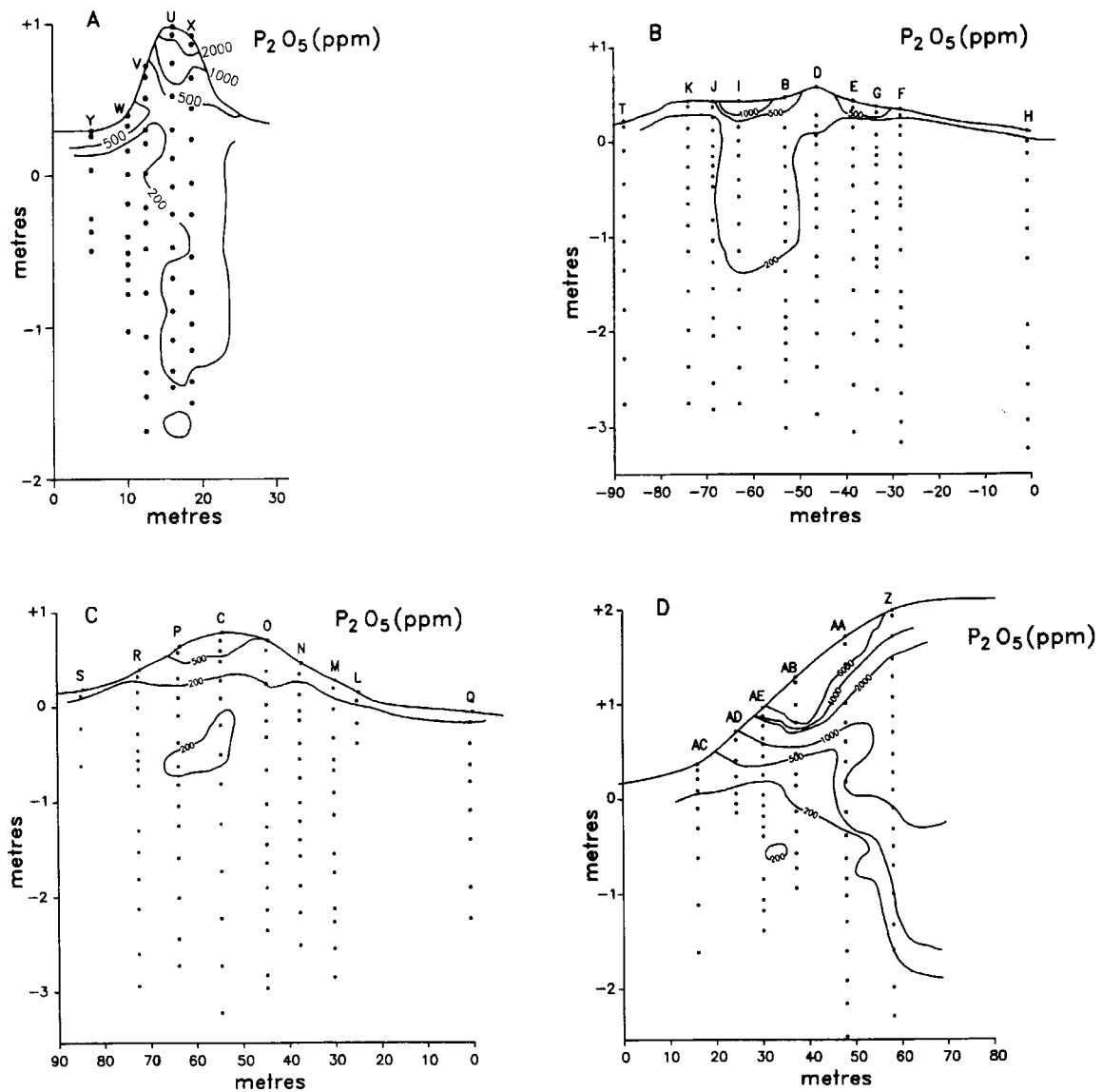


Figure 12. Distribution of phosphorus in island soils; concentration contours in ppm  $P_2O_5$ . (A) Small island; (B) Imperata island; (C) Phoenix island; (D) Hog island. Dots show sampling points in each of the auger holes or pits. Vertical axis is sample elevation relative to local datum (Figure 2a), and horizontal axis shows horizontal distance between holes. See Figure 2a for location of profiles

Table II. Results of *R* mode factor analysis on combined chemical data

	Factor 1	Factor 2	Factor 3	Factor 4
Fe	0.270	0.802	0.134	0.339
Al	0.184	0.308	0.049	0.930
K	0.510	0.527	0.466	0.639
Ca	0.909	0.529	0.251	0.179
P	0.221	0.124	0.960	0.035
Eigenvalue	3.190	0.921	0.422	0.314
Variance (%)	63.8	18.4	8.4	6.3

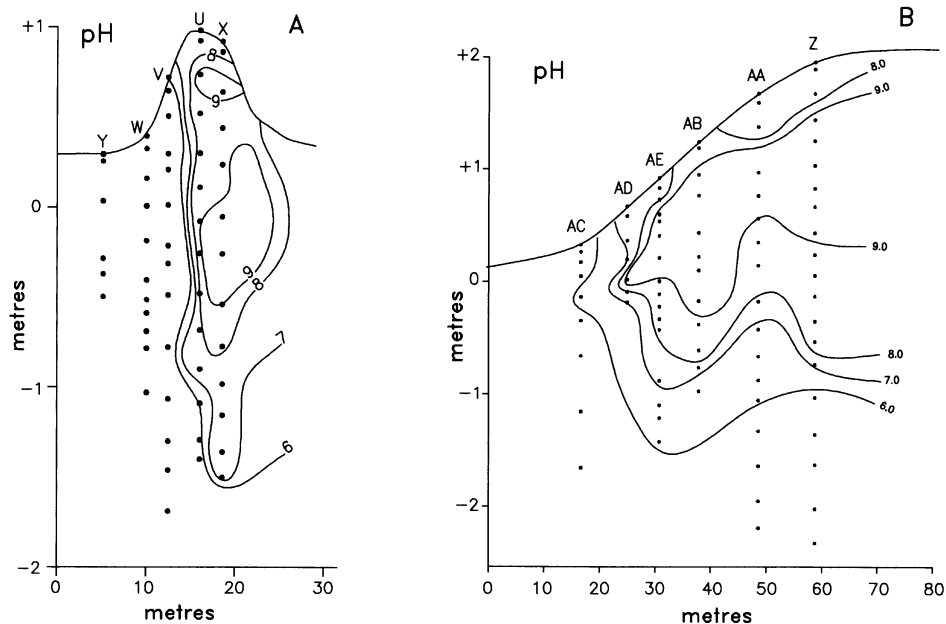


Figure 13. The pH of island soils; contour interval in pH units. (A) Small island; (B) Hog island. Dots show sampling points in each of the auger holes or pits. Vertical axis is sample elevation relative to local datum (Figure 2a), and horizontal axis shows horizontal distance between holes. See Figure 2a for location of profiles

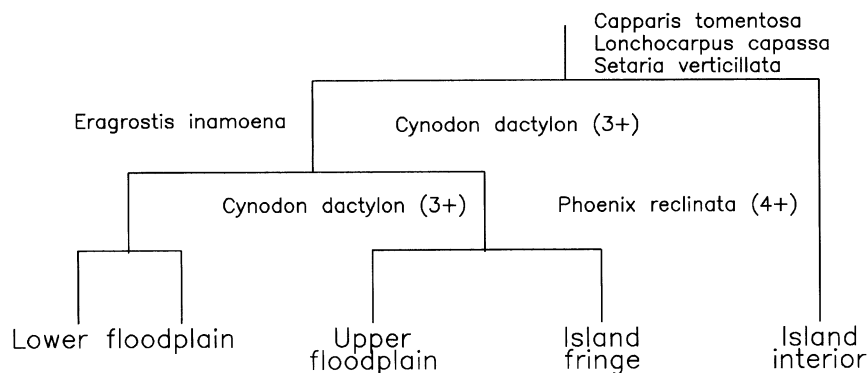


Figure 14. Dendrogram showing vegetation classification in the study area. See text for details

communities in areas which are not flooded at all (Figure 16). The distribution of island edge and island interior communities is probably related to soil and ground water chemistry, as has been illustrated in other studies in the Okavango region (Ellery *et al.*, 1993).

#### Faunal activity

Small island is an eroded mound, built by the fungus-growing termite *Macrotermes michaelseni*. Mounds normally consist of a turret, which houses the ventilation system, and a pediment which is formed by erosion of the turret by rain (Figure 17). Once a colony dies, usually through ant predation or waterlogging, the epigeal turret is no longer maintained and degrades, being washed down onto the pediment (Pomeroy, 1989). The pediment forming Small island consisted of bare soil, on which two *Trinervitermes* spp. colonies had established and produced secondary domes *c.* 40 cm in diameter and 15 cm high. Foraging by *Microtermes* spp. beneath carton was extensive on the fringes of the pediment, whilst disturbance by burrowing mammals was absent from the island and immediate surrounds.



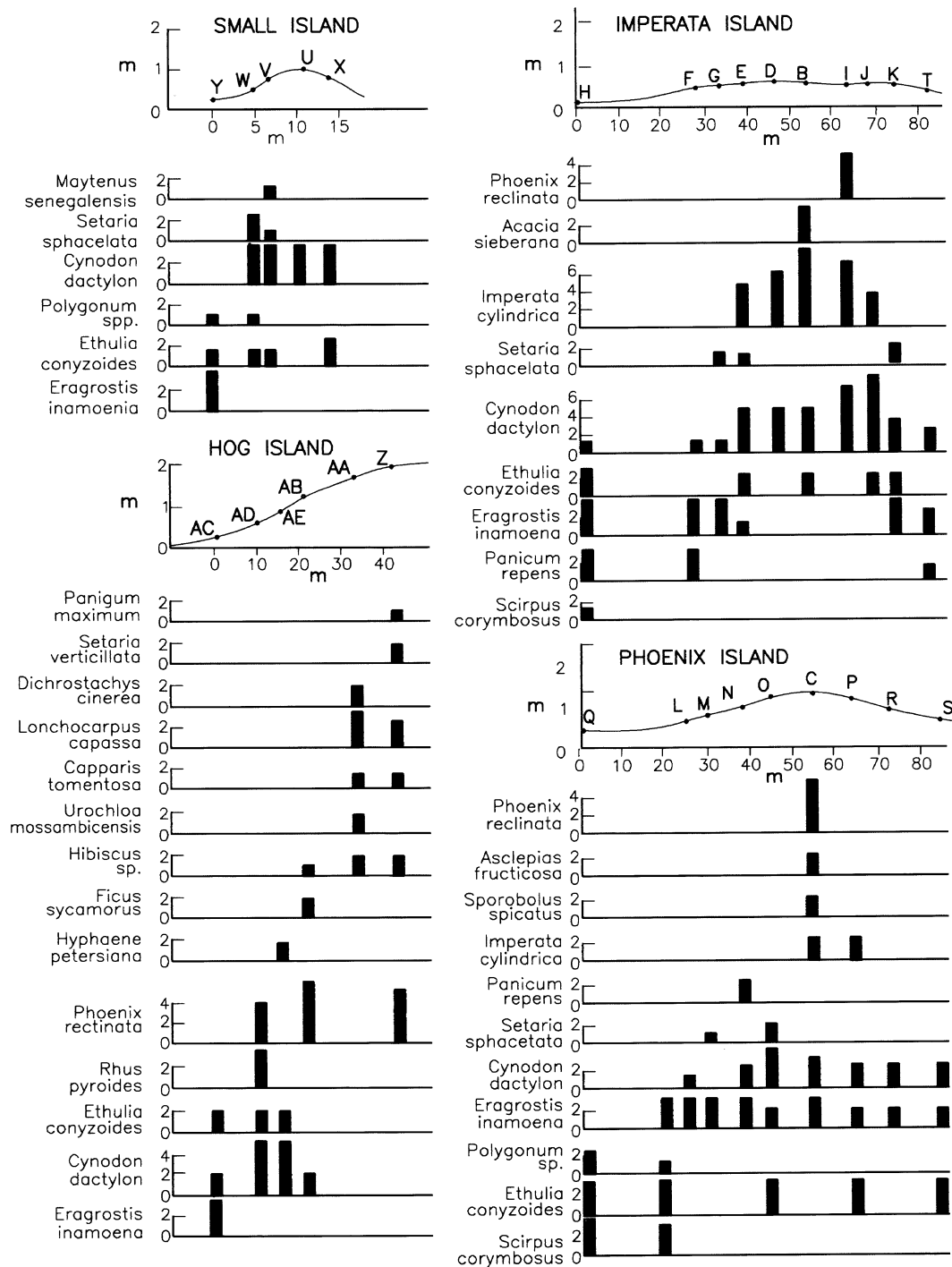


Figure 15. Species zonation across each of the islands in the study area. Species abundance is rated on a seven-point scale. See text for details

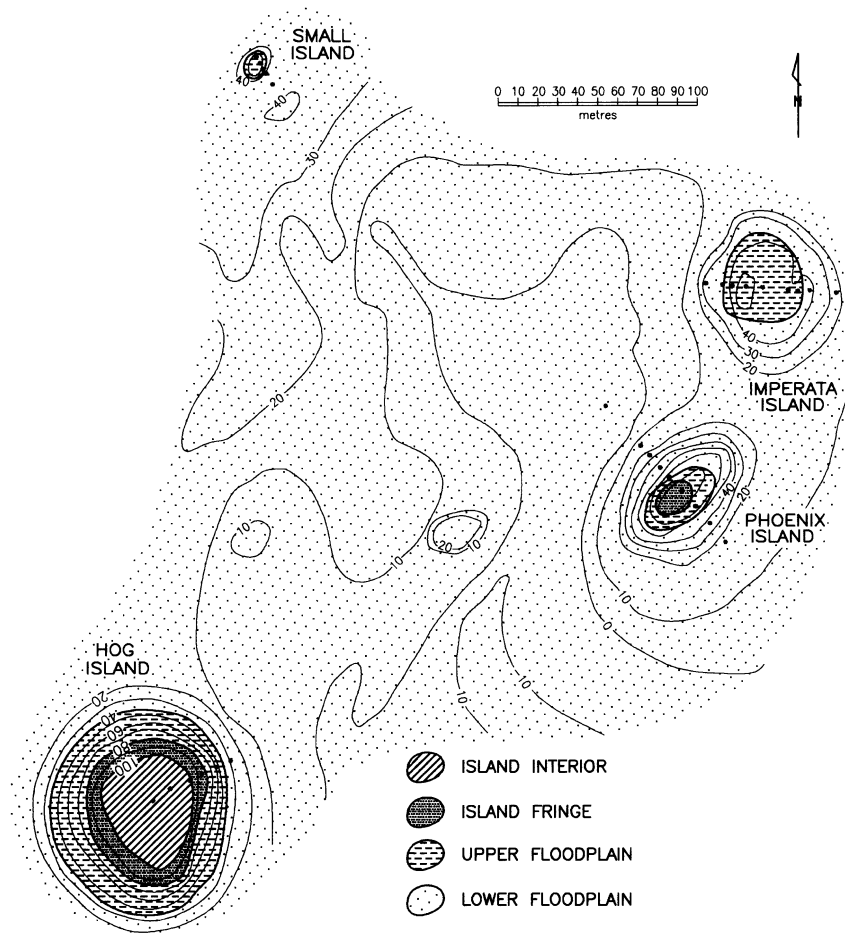


Figure 16. Vegetation map of the study area

The larger Imperata island also contained a dead mound of *M. michaelsoni*, although this was less eroded, and had greater surface expression than the low dome of Small island. Excavations revealed the typical shelving system of the fungus garden in a chamber, the base of which was 85 cm above the level of the floodplain. No fungus or termites were observed, except for an active commensal colony of *Microtermes* sp. The mound was shaded on three sides by a dense stand of *P. reclinata*, a species of palm, which appeared to be established on the pediment. The adjacent Phoenix island had, at its centre, a mature *M. michaelsoni* mound, with a well developed turret rising about 4 m above the floodplain. A breach made in the turret exposed a major vent in which several minor and occasional major soldiers were observed. The damage to the vent was repaired within 4 h.

On Hog island, three active and two inactive mounds were present, activity being confined to the outer margin of the island, and associated with the Phoenix palm fringe. One of the mounds was actively prograding, adding around 15 per cent to the volume of the existing 100 cm tall turret in 24 h. At least three of these mounds had been burrowed into by aardvark (*Orycteropus afer*). Elephants (*Loxodonta africana*) had opened pathways between the mounds to access Phoenix palm fruits. Several ant species, including both seed-eating and carnivorous types, were common on the island, together with various beetles (*Coleoptera*), burrowing crickets (*Gryllidae*), silverfish (*Thysanura*) and woodlice (*Oniscidae*), observed in a cursory search of the organic-rich, relatively unconsolidated topsoil. *Microtermes* spp. were abundant on the extremities of the island beyond the fringe of Phoenix palms, but occurred less frequently in the centre of the island. Soil dumps and foraging groups of the harvester termite, *Hodotermes mossambicus*, occurred on the island, the island fringes and the floodplain

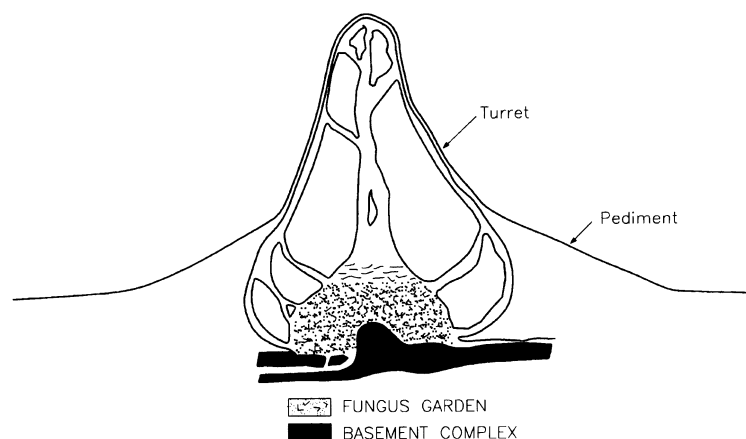


Figure 17. Schematic cross-section through a termitarium

to the southeast. In many places, this outer fringe was disturbed by foraging activities of warthogs (*Phacochoerus aethiopicus*) which commonly use both snout and tusks to excavate roots, stolons and tubers, and in the study area, the stolons of the grass *Cynodon dactylon* are preferred food. Although not specifically measured, it appeared that active or inactive *Macrotermes* mounds make up a progressively smaller proportion of the surface of the island with an increase in island size.

Away from the islands throughout the floodplain, extensive foraging by *Microtermes* spp. on litter, standing dead grass, live grass and mammalian dung, especially of elephant, was observed. Ant colonies of several species were also common, recognized by one or more access holes to subterranean burrows. Soil dumps and foragers of *H. mossambicus* were also present but in discrete, roughly circular patches of around 40 to 50m radius, which probably defined isolated colonies of this species. Grass and herbaceous litter was much reduced within these patches, but there was no obvious influence on topography. Occasionally, disturbance to areas of around 0.3ha were made by burrowing mammals. Two types were distinguished: (1) deep holes with wide entrances, and spoil heaps of subsoil made by aardvarks, honey badgers (*Mellivora capensis*) and warthogs, but utilized by a range of other species, including spotted hyena (*Crocuta crocuta*), aardwolf (*Proteles cristatus*) and pangolin (*Manis temmincki*); and (2) smaller, more frequent burrows with less extensive spoil heaps formed by various species of rodent and mongoose. A by-product of foraging by moles and mole rats is linear arrays of spoil heaps, generally less than 20cm high, but because of the sandy, cohesionless nature of the subsoil, these are ephemeral. These various mammal species do not produce durable topographic expressions, as the sand heaps they create are rapidly dispersed by trampling and by rain storms, because the sand lacks cohesion.

#### *Patterns of colonization by plants*

There is a positive relationship between island size and the number of woody plant species on each island (Figure 18). This habitat diversity is well illustrated in the variety of flooding conditions and soil chemical compositions illustrated in this study (see below). Ground water salinity may also contribute to habitat differences, as described by Ellery *et al.* (1993).

Mechanisms of seed dispersal appear to account for many of the differences in the patterns of colonization of islands by woody plants (Table III). Initially it appears that seeds are spread by antelope (probably impala), which are mixed feeders (i.e. they browse on woody plants and graze on grasses and grass-like plants such as sedges), and/or primates (monkeys and baboons which often eat fruits of dicotyledonous plants). These animals are frequently to be seen on the open floodplain habitats. Once these early plant colonizers have established, bird dispersal becomes more important, with fruit-eating birds perching on trees on small islands and dispersing

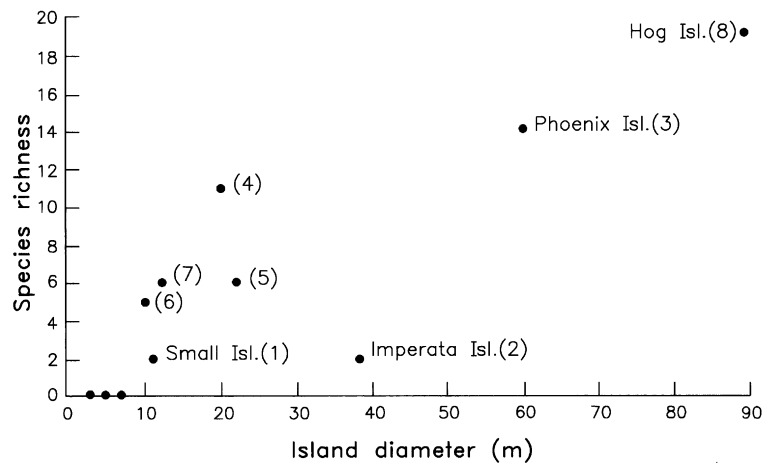


Figure 18. Species richness (woody plants only) as a function of island size in and around the study site

Table III. Occurrence of woody plant species on eight islands in the study area (P denotes present), and their seed dispersal mechanisms. Island numbers refer to the data plotted in Figure 18

Plant species	Island								Dispersal agent
	1	2	6	7	5	4	3	8	
<i>Croton megalobotrys</i>								P	Elephants
<i>Sclerocarya birrea</i>								P	Elephants
<i>Hlphaene petersiana</i>								P	Elephants
<i>Ximenia americana</i>								P	Primates
<i>Boscia albitrunca</i>								P	Birds, mammals
<i>Euclea divinorum</i>								P	Birds
<i>Rhus quartiniana</i>								P	Birds
<i>Combretum mossambicense</i>								P	Wind
<i>Grewia discolor</i>							P		Birds, mammals
<i>Phyllanthus</i> sp.							P		Birds
<i>Lonchocarpus capassa</i>							P	P	? Antelope
<i>Ficus natalensis</i>						P			Bats, birds, other mammals
<i>Ficus capreifolia</i>					P				Bats, birds, other mammals
<i>Ficus sycamorus</i>					P	P	P	P	Bats, birds, other mammals
<i>Rhus pyroides</i>					P	P	P	P	Birds
<i>Vernonia amygdalina</i>					P		P	P	Wind
<i>Dichrostachys cinerea</i>				P				P	Antelope
<i>Diospyros lycioides</i>				P		P			Antelope, birds, primates
<i>Diospyros mespiliformis</i>				P		P	P		Antelope, birds, primates
<i>Jasminum fluminense</i>				P		P	P	P	Birds
<i>Capparis tomentosa</i>			P			P	P	P	Primates
<i>Securinea virosa</i>			P	P		P	P	P	Birds
<i>Ziziphus mucronata</i>			P			P	P		Antelope, birds
<i>Acacia sieberana</i>		P					P	P	Antelope
<i>Phoenix reclinata</i>		P			P	P	P	P	Antelope, birds, primates
<i>Maytenus senegalense</i>			P	P	P	P		P	Birds
<i>Acacia tortilis</i>	P		P				P		Antelope

seeds. At a later stage elephants become the main agents of dispersal, moving between large islands in the dry season in search of browse.

### Termitaria

Termite activity has been cited as a cause of mounded topography and for this reason samples of termitaria were collected and subjected to mineralogical and chemical analysis. Termites construct their mounds using sand grains which are cemented together with a mortar consisting of fine material (Lee and Wood, 1971;

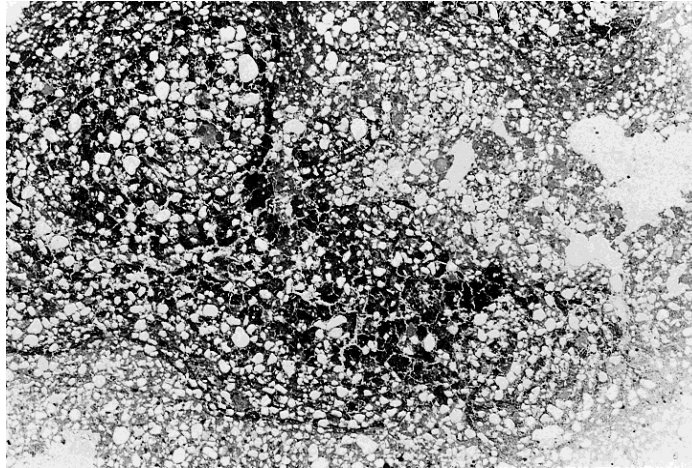


Figure 19. Photomicrograph of a thin section through portion of a termitarium. See text for details. Field of view is 2 cm wide

Table IV. Chemical analyses of material from termite mounds (data expressed in weight percentage)

	1 Ant 1	2 Ant 2	3 Ant A	4 Ant 2 – 74 µm
SiO <sub>2</sub>	87.57	79.69	91.64	49.87
TiO <sub>2</sub>	0.18	0.21	0.22	0.30
Al <sub>2</sub> O <sub>3</sub>	2.63	3.25	3.56	6.71
Fe <sub>2</sub> O <sub>3</sub>	1.54	1.79	0.78	4.46
MnO	0.07	0.08	0.06	0.12
MgO	0.60	1.03	0.29	2.14
CaO	1.91	4.09	0.10	11.01
Na <sub>2</sub> O	0.05	0.06	0.07	0.14
K <sub>2</sub> O	0.35	0.38	0.15	1.02
P <sub>2</sub> O <sub>5</sub>	0.11	0.11	0.08	0.18
LOI	5.87	9.55	2.90	23.90
<b>TOTAL</b>	<b>100.87</b>	<b>100.25</b>	<b>99.85</b>	<b>99.86</b>
Illite	3.0	3.2	1.3	8.6
Kaolinite	3.8	5.1	6.6	8.6
Limonite	1.5	1.8	0.8	4.5
Calcite	4.7	9.5	0.8	24.1
Quartz	83.8	76.0	89.0	42.9
Organic material	3.2	4.4	1.5	11.3

Mermut *et al.*, 1984; McCarthy *et al.*, 1986) mixed with body fluids. The photomicrograph of a thin section through a portion of a termitarium in Figure 19 shows two types of mortar, one rich in iron oxide and clay (dark) and the other calcite rich (pale). Each sand grain is surrounded by the mortar material.

The chemical composition of soil from a small, active *M. michaelsoni* mound from the floodplain (Table IV, column 3) is dominated by silica, reflecting the fact that by volume, quartz sand makes up most of the anthill (about 89 per cent). Compared to the A soil horizon (Table I, columns 1 to 3), the mound soil is higher in aluminium, indicating that the termites have imported clay for the construction of the termitarium, and possibly other fine grained materials such as quartz. The increase in clay content is fairly small, but nevertheless represents a doubling of the clay content compared to normal A horizon soil. Calcium is low, however, probably due to the very low abundance of calcite in the floodplain environment. Termitaria from Phoenix island (Table IV, column 2) and Hog island (Table IV, column 1) are enriched in Fe, Al and Ca relative to floodplain material, indicating that clay, limonite and calcite have been used for construction.

Mortar material was separated from a sample of mound soil from Phoenix island by gentle crushing and sieving to remove material larger than 74 µm (3.75 phi), which includes most of the sand grains (Figure 3).



Figure 20. Photograph of an excavated termite mound. The turret height is 20cm

Silica abundance is reduced, and iron, aluminium and calcium enriched in the fine fraction (Table IV, column 4), indicating high proportions of clay, limonite and calcite in the mortar material. Nevertheless, quartz still forms the largest single component of the mortar (42.9 per cent), indicating that the termites also make use of fine silica particles in their constructions.

Serial excavation of a small termitarium on the floodplain revealed several fungus chambers below ground level beneath and connected to the turret by galleries. The chambers and galleries were lined with darker coloured clay- and limonite-rich material, presumably to ensure stability in the generally sandy substrate. There was also evidence that several chambers and galleries had been back-filled with this darker material (Figure 20).

## DISCUSSION

The substrate underlying the floodplain consists of fine, well sorted sand (Figure 3), probably of aeolian origin. This material is very low in clays and other fine grained particulates, although a slight enrichment in fines, consisting mainly of clays, occurs in a thin A soil horizon developed on the plain. The source of these fines is unknown, but fluvial transport during periodic flooding is likely, or it may be wind-borne material. Islands have developed on this plain and vary in size, in floral composition and in faunal activity.

It seems that islands grow much faster in diameter than in height: the largest island in this study is twice the height of the smallest, but at least 10 times the diameter (Figure 2). The increase in island size is associated with changes in the mineralogical constitution of its soils as well as in the associated floral and faunal assemblages.

The smallest island shows a distinct increase, albeit small, in fines compared to both the white sand and the A soil horizon of the floodplain, primarily because of an increase in clay content beneath the island (Figure 6). A mineral phase, probably calcite, is also a part of the component of fines concentrated in this way. The more clay-rich soils have, however, been augmented in fines by further addition of calcite.

Mound-building termites use fine material for construction of nest structures including the turret, lining of galleries, and for back-filling of redundant cavities. The termite mound sampled on the floodplain showed an increase in clays, presumably gathered from the surrounding A soil horizon (Table IV, column 4). In addition,

the termites have also collected fine grained silica for this purpose. Consequently the most likely cause of the increase in fines beneath Small island is termite activity.

The species responsible for this process is *M. michaelseni*, to date the only species recorded in the Okavango that constructs large epigeal nests (Schoorman and Dangerfield, 1996). *M. michaelseni* colonies begin when a male and female reproductive or alate pair dig a small burrow in moist soil after a major rainfall event. Eggs are laid and tended by the pair until a brood of workers is produced which is able to forage and establish a fungus garden. Subsequent broods that include workers and soldiers are produced, and the colony expands to several thousand individuals with a fungus garden as much as 15 cm in diameter (Abe and Darlington, 1985). The base of the fungus chamber may be up to 50 m below surface and galleries may extend downward to 85 cm, but there is no epigeal expression or evidence of the colony's presence. At some critical point, perhaps related to moisture or temperature control of the internal nest environment, an epigeal turret is constructed (Figure 17), initially very quickly and then more steadily, until in mature mounds it reaches 4 m above ground level (e.g. Schoorman and Dangerfield, 1996). The soil material for this turret is collected from galleries around the nest and from deep soil horizons (see review by Garnier-Sillam, 1989).

Once above ground, rain erodes the turret and an outwash pediment is created (Figure 17). Estimates of erosion rates vary (Pomeroy, 1976) but may be as high as  $1 \text{ mm ha}^{-1} \text{ a}^{-1}$  of eroded soil (Lepage, 1984). Termite workers continue to maintain the turret, adding material from the surrounding soil, and may move large quantities of soil laterally in order to expand the turret size.

At almost any time, but especially in these early stages, colonies are vulnerable to ant predation (Collins, 1981; Lepage, 1991) and mortality due to flooding. Erosion rates may increase if the colony dies, but a raised pediment remains a permanent feature of the habitat because soil for its construction has been gathered from a wide area. It seems likely that Small island represents such an eroded pediment.

The increase in fines, notably clays, initially favours run-off, but later improves the water retention properties of the soil; moreover, the activities of termites and commensal species results in localized enrichment of nutrients in the soil (Fanshawe, 1968; Arshad, 1982; and Figures 11 and 12). The combination of less frequent flooding and nutrient enrichment on termite mounds would increase palatability and overall forage quality for herbivores. Grasses such as *Cynodon dactylon*, which colonize these areas early on (Figure 15), would attract grazing animals such as the red lechwe (*Kobus leche*) and impala. Equally important in the case of the Okavango floodplain is the elevation of the mound, which provides a micro-habitat free from the effects of flooding, and which therefore enables the growth of small trees. Initially small shrubs colonize the mound, as in the case of Small island, and later Phoenix palms (Figure 15).

The presence of these woody plant species has a profound effect on the island, primarily as a result of transpiration, which concentrates solutes in the ground water beneath islands, leading to the precipitation of silica and especially calcite (McCarthy *et al.*, 1993). Beneath Small island, clays are an important component in the soil while calcite is less so (Figure 6 and 7), while beneath the larger islands, clays are less important, having been diluted as a result of the precipitation of calcite and probably silica. In the case of Hog island, the largest in the present study, calcite makes up the major component of the fine fraction, and in some samples constitutes as much as 15 per cent of the soil.

Pre-existing mounds would provide sites for subsequent successful colonization because the risk of flooding is reduced and there is a greater abundance of fines and food. The overall effect of colonization by successive generations of termites and precipitation of calcite and silica from ground water is to cause the islands to grow. Islands situated close together may merge, as in the case of Phoenix and Imperata islands. Over time, therefore, the islands grow both in diameter and in height. Differences between islands of different size therefore reflect different stages in the evolution of the islands, and are a consequence of the processes responsible for island construction.

The pattern of colonization of islands by plants appears to be partly related to stochastic patterns of seed dispersal (Table III). However, the overall pattern follows a sequence which depends on dispersal by different guilds of organism. Initially, colonization is by plants which have seeds dispersed by antelope. Pods of many acacia form an important part of the diet of ungulates, particularly during the dry season when the amount of forage is low, and several species, such as the impala and red lechwe, typically wander around the floodplain in search of food. They spend more time on elevated mounds where forage quality is higher than the surrounding

floodplains. Primates (baboons and vervet monkeys) may also be important in dispersing seed to these areas, although they tend to spend less time in floodplain habitats where they are visible to predators.

The early woody plant colonizers are typically fast-growing species (e.g. various species of acacia), and once established on islands are used by birds as perches. Fruit-eating birds then become important agents of dispersal, and may be responsible for the appearance of species which produce fleshy fruits such as *Maytenus senegalensis*, *Securinega virosa* and several species of fig (*Ficus* spp.). Finally, elephants act as important agents of dispersal, often along well defined paths, and wander about on islands in search of food. Preferred islands would be sufficiently large to provide adequate reward for search effort, and therefore those plant species dependent on elephants for dispersal, such as *Hyphaene petersiana*, would be found only on larger islands.

The presence of shrubs and palms, as well as termites, on the islands attracts insect, mammal and bird species, as the islands then provide a source of both food and shelter. These animals import nutrients and, together with the burrowing activities of mammals and soil invertebrates, further enhance the nutrient status of island soils relative to those of the floodplain (e.g. Figures 11 and 12), thus sustaining the dense vegetation growth on the islands.

The later plant succession and distribution on larger islands is related to progressively more saline ground water towards the island interior, a phenomenon which we attribute to the effects of transpiration (Ellery *et al.*, 1993; McCarthy *et al.*, 1993; McCarthy and Ellery, 1995). Increase in salinity is accompanied by an increase in alkalinity, as the dominant solute is sodium bicarbonate. It is this increase in salinity which induces the calcite precipitation, particularly beneath the island margins. Larger islands generate greater concentration gradients than small islands, because they have more trees.

Phoenix palm has a low salinity tolerance (Ellery *et al.*, 1993), while most woody species exhibit moderate tolerance. The appearance of a break in the phoenix cover in the interior of the islands as they enlarge is therefore attributed to salinization of the ground water. This break in cover is exploited by more salt-tolerant species, which colonize the interior of the larger islands. Larger islands therefore have a higher species diversity (Figure 18). Soils in the interior tend to become alkaline, as saline water migrates to the surface by capillarity and evaporates. Termites continue to forage in these areas, but termitaria are absent, probably because of the sensitivity of the termite fungus gardens to alkaline water. However, under present conditions in the study area, soil pH itself does not appear to have a significant effect on vegetation zonation, because all of the islands in the present study have similar soil pH structure (Figure 13). Rather, we believe it is the rise of alkaline, saline ground water during periodic flooding which maintains vegetation zonation on the islands, and impacts on termite mound distribution.

It has been shown that the salinity gradient beneath islands causes calcite precipitation to be confined primarily to the outer margins, with little taking place in the island interior (McCarthy *et al.*, 1993). Islands therefore appear to grow laterally at a faster rate than vertically, and in larger islands there is probably little vertical growth by chemical precipitation. Vertical growth in such areas is probably confined to dust accumulation, as the tree-covered islands would serve as efficient dust traps during the dry season. The elevation of islands above the floodplain may well be self-limiting, controlled by the compositional gradients in the underlying ground water.

The results of the factor analysis (Table II) are consistent with the evolutionary scenario developed above. Factor 1, dominated by Ca, represents the precipitation of calcite, which is the major agent in island growth. Factor 2 reflects the precipitation of Fe, which is induced by plants. Plants require oxygen in the vicinity of roots. If the water table rises, oxygen is rapidly depleted by micro-organisms, leading to anoxic conditions. Wetland plants are adapted to this by having aerenchyma which conduct atmospheric gas to the roots. Certain non-wetland plants can produce these rapidly on flooding, and release oxygen from the roots, thereby maintaining an oxygenated environment. This oxidizes iron in the ground water, precipitating iron hydroxide in the vicinity of the roots (Marschner, 1986). It appears that this iron oxide preferentially nucleates on clays in Okavango soils. This phenomenon has been reported previously (Fordham, 1970), but is not universal (Schwertmann, 1988). The local enrichment of iron thus created may well have a beneficial side effect, in that it protects the island vegetation from chlorosis as the ground water becomes more alkaline (Marschner, 1986). Factor 3 is associated with P. The localization of P to the upper soil horizons (Figure 12) suggests that



importation of P by insects and especially animals is the major agent responsible. Finally, Factor 4 is associated primarily with Al, and less with Fe, and represents the clay component accumulated by termites. In contrast to the above, K is spread amongst all four Factors, which suggests multiple sources: as a component of clays (Factor 4), imported along with P (Factor 3), and precipitated from the groundwater as potassium feldspar (McCarthy *et al.*, 1991) (Factors 1 and 2). The spatial distribution of K, i.e. concentrated both in the upper soil horizon and towards island centres (Figure 11), is consistent with this interpretation.

It is well known that the activities of termites result in local nutrient enrichment in soil (Fanshawe, 1968; Arshad, 1982). However, what has emerged from this study is that nutrients continue to accumulate on islands even after termite activity has become a secondary process in island growth. The largest (Hog) island shows the greatest nutrient enrichment relative to the floodplain, namely a six-fold enrichment in Fe and 30-fold enrichment in K and P. All of these nutrients are essential in sustaining the greater biological productivity of islands. It thus appears that termites initiate a process which ultimately becomes both self-sustaining and self-enhancing, which leads to the progressive growth of islands.

## CONCLUSION

Islands in the wetlands of the Okavango result from a dynamic interaction between the biota and the physical environment. It appears that the process of island construction is initiated by the termite *M. michaelseni*, which creates a nucleus in the form of a turret above its subterranean fungus garden. In order to do this, it is necessary for the termites to import fine grained materials, particularly clays, from the surrounding area. These change the physical properties of the soil in the mound. The elevation of the mound and its improved soil characteristics create a micro-habitat which supports vegetation of higher forage quality than the surrounding floodplain. This in turn attracts mixed browsing and grazing ungulates, and as a result shrubs and trees become established on the mound. The presence of these plants results in an increased transpiration rate from the island, and the underlying ground water becomes increasingly saline, to the point where saturation in calcite is attained. The precipitation of this mineral in the soil beneath the island results in expansion, and hence island growth. As the island grows in size, an increasingly wide range of habitats is created, probably due primarily to an increase in the salinity gradient in the underlying ground water. This results in an increasingly diverse flora on the islands. It is likely that mammals, attracted to the island in search of both food and shelter, are responsible for the introduction of these plant species. The activities of plants and animals result in a continual increase in soil nutrient levels. Thus, the initial activity of a single species sets in motion a complex successional sequence involving plants, mammals and the geohydrological and geochemical regimes, the outcome of which is the undulating topography of the floodplains of the Okavango fan.

Jones *et al.* (1995) describe such effects of biota on physical properties of the environment as 'ecosystem engineering'. One organism, the engineer, directly or indirectly modulates the availability of resources for other organisms in the ecosystem and thus affects community structure and function. Engineering by *M. michaelseni* in the Okavango delta initiates successional and geochemical processes that become self-enhancing, and not only determine local plant species composition and vegetation mosaics, but also define the physical structure of the landscape.

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